

Formation of plications in the Miocene bivalve *Mytilus* (*Plicatomytilus*) *ksakurai* as a consequence of architectural constraint

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Received 7 March 1998; Revised manuscript accepted 2 November 1998

Abstract. A total of 68 specimens of thick-shelled, peculiarly shaped Miocene mytilids from Hokkaido and northern Honshu were examined from the viewpoint of constructional morphology. They have been treated as members of three species: *Mytilus* (*Plicatomytilus*) *ksakurai*, *M. (Tumidimylus) tichanovitchi*, and *M. (T.) furanuiensis*, with different shell shapes, muscle scars and surface sculpture. *M. ksakurai* shows an abrupt increase in shell convexity during ontogeny, like that in *M. tichanovitchi*. It develops a few conspicuous plications just after this allometric change in shell convexity. Polished sections of the shell of *M. ksakurai* reveal that just after the abrupt change in shell convexity, the internal growth increments bend sharply toward the inside of the shell. This is associated with a remarkable thickening of the outer part of the fibrous prismatic layer of the shell. These facts suggest that in *M. ksakurai*, the mantle turned inward at the stage of the allometric change in shell convexity. Consequently, the diverging plications were formed by the wrinkled mantle as a result of the reduction in space across which the mantle extended.

Key words: allometric change, mantle bending, *Mytilus ksakurai*, plication, tablecloth wrinkle

Introduction

The tempo and mode of morphological evolution in fossil organisms can be inferred by analyzing changes in fossilized hard tissue through geologic time. Realization of the rule of constructional processes of hard tissue structures is important for better understanding their morphological evolution.

A number of works deal with pattern formation in molluscan shell sculpture from the viewpoint of constructional morphology (e.g., Seilacher, 1972) and theoretical morphology (e.g., Macomber and Macomber, 1983; Hayami and Okamoto, 1986; Gunji, 1991; Ackerly, 1992). However, little is known about how shell sculpture is formed, although several hypotheses have been proposed by previous authors (e.g., Cox et al., 1969; Hayami, 1974; Seilacher, 1985). Hayami and Okamoto (1986) pointed out that the formation of striae in the shell of the scallop *Camptoneustes* may be related to the direction of crystal growth of foliated calcite.

Divergent ribs are one of the characteristic features of bivalve shells. During Early to Late Miocene time, peculiarly shaped mytilids flourished in the North Pacific region. Among them were forms with a plication or several diverging plications, described under the subgenus *Mytilus* (*Plicatomytilus*) by Allison and Addicott (1976) (Figure 1-3, -4, and -5). During the same time interval, several non-plicated but similarly thick-shelled *Mytilus* species (Figure 1-1

and -2) occurred in the same paleozoogeographic realm. Kafanov (1984) proposed the subgenus *M. (Tumidimylus)* for these forms. These plicated and non-plicated mytilids have been considered to be closely allied to each other phylogenetically (Noda and Hoyanagi, 1993).

The process and factors controlling formation of plications in *M. (Plicatomytilus)* are analyzed here on the basis of microscopic observations of shell cross-sections and biometric analysis of shell form. The paper focuses on how the plication is formed in relation to mantle behavior.

Materials

Lower and Middle Miocene marine strata in Hokkaido and northern Honshu yield abundant shallow cold-water molluscan fossils known as the Asahi and Chikubetsu faunas respectively (Chinzei, 1978). The faunas typically include thick-shelled, peculiarly shaped mytilids that have been classified as species of *Mytilus* (*Plicatomytilus*) and *M. (Tumidimylus)*. The following five species have been described from Sakhalin, Hokkaido, and northern Honshu: *M. tichanovitchi* Makiyama, 1934, *M. furanuiensis* Uozumi and Akamatsu, 1988, *M. ksakurai* Nomura and Hatai, 1936, *M. (P.) hidakensis* Suzuki, Sakai, and Uozumi, 1983, and *M. (P.) monbetsuensis* Uozumi and Akamatsu, 1988. Related species in these two subgenera are also known from the

Miocene of Kamtchatka, Alaska, and California, indicating that these mytilids were widely distributed throughout the North Pacific paleozoogeographic realm.

In this study, 68 specimens of these Miocene mytilids were analyzed from the viewpoint of constructional morphology. Specimens of three extant non-plicated *Mytilus* species, *M. (Mytilus) galloprovincialis*, *M. (M.) californianus* and *M. (Crenomytilus) grayanus* were also studied for comparison. Localities and stratigraphic horizons from which the samples came are listed in Table 1.

Specimens of *M. (Plicatomytilus)* were collected from outcrops exposed in the Katsura River, Aomori Prefecture, northern Honshu, and in the Kishimatsu-zawa River, southern Hokkaido. The Katsura River is the type locality of *Mytilus ksakurai*, and the Kishimatsu-zawa River that of *M. monbetsuensis*. According to the original description by Nomura and Hatai (1936), *M. ksakurai* is characterized by a thick, extremely convex shell without plications. Noda and Motoyama (1991) reported specimens referable to *M. hidakensis* from the type locality of *M. ksakurai*. *M. hidakensis* was described on the basis of specimens from Urakawa Town, Hidaka Province, southern Hokkaido. It is characterized by a thick, highly convex shell with three strong plications. Noda and Hyanagi (1993) suggested that the specimens described as *M. ksakurai* are juvenile specimens of *M. hidakensis*. Subsequently, Noda (1994) interpreted *M. hidakensis* as a junior synonym of *M. ksakurai* based on the presence of a plication preserved in relief on the inner mold of the holotype of *M. ksakurai*, and assigned *M. ksakurai* to the subgenus *M. (Plicatomytilus)*.

Uozumi and Akamatsu (1988) described *M. monbetsuensis* from a Middle Miocene outcrop in the Kishimatsu-zawa, a branch of the Kabari River, Monbetsu Town, Hidaka Province, Hokkaido. This species is similar to *M. hidakensis* but is distinguished from that species by having a single plication, weaker than the three in *M. hidakensis*, and a slightly concave dorsal margin. However, in the same way as does *M. (P.) gratacap* described by Allison and Addicott (1976),

specimens collected at localities in the Katsura and Kishimatsu-zawa Rivers exhibit wide variation in the number and strength of plications (Figure 1-3, -4, and -5, Figures 2 and 9), including morphotypes assignable to both *M. hidakensis* and *M. monbetsuensis* (see Figures 1-3, -4, and -5, Figures 2 and 9). These specimens are, therefore, regarded as belonging to a single species showing wide variation in shell morphology. They are classified as *M. ksakurai* in this paper.

All the specimens utilized are housed in the University Museum, University of Tokyo (UMUT).

Methods

For microstructural observation, single valves of both extant and fossil specimens were cut along the maximum growth axis. The sectioned surfaces were polished with graded series of carborundum and alundum, coated with clear nail varnish, and observed under a binocular microscope.

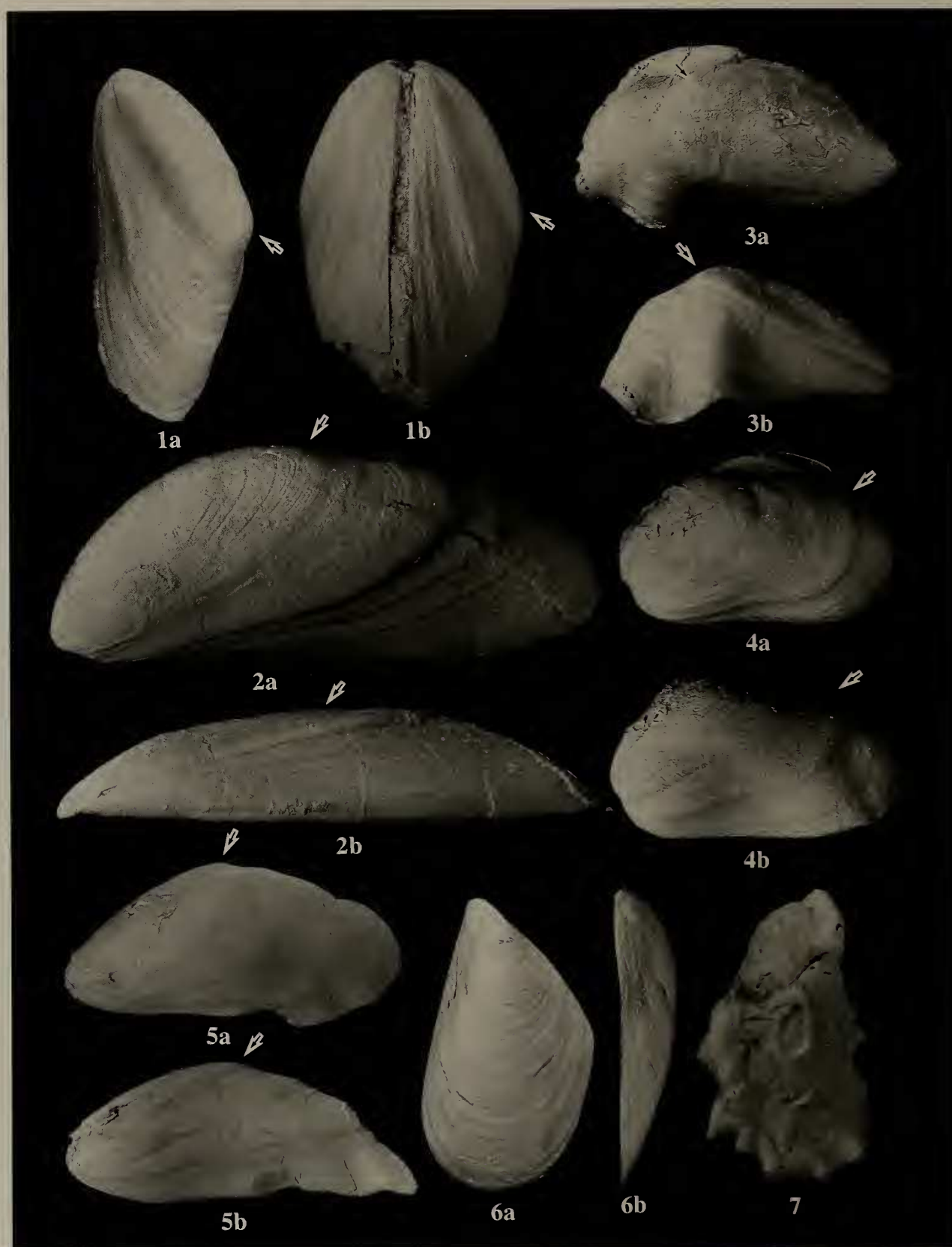
In all double scatter diagrams, 95% confidence intervals of the data are represented by horizontal and vertical bars.

This study focuses on four aspects of the shell of *Mytilus*. They are: a) morphological features of the commissure plane (generating curve), b) whorl expansion rate, c) secretion rate of the outer part of the fibrous prismatic layer, and d) degree of plication development.

To realize aspect a), four variables were measured. They are: 1) the shape of the generating curve (Raup and Michelson, 1965), that is, lengths of major and minor axes of the commissure plane approximated as an ellipse, 2) position of the break point on the commissure (explained below), 3) distance between the hinge axis and the break point on the commissure at which plications begin to appear, or at the stage of the allometric change in shell convexity, and 4) curvature of each segment of the commissure. 1) is utilized to understand the overall morphological characters of the commissure plane. 3) and 4) are utilized to understand the

Table 1. List of the materials utilized. The numbers in parentheses represent the numbers of specimens used in measurements of all variables. Ages after Kimura and Tsuji (1992) for Takinoue Formation and Noda (1994) for Furanui and Isomatsu Formations.

Species and related species	Number of specimens	Horizon and age	Locality
<i>Mytilus (Mytilus) galloprovincialis</i> Lamarck, 1819	7(6)	Recent	Nojima Coast, Yokohama City, Tokyo Bay, central Japan
<i>M. (M.) californianus</i> Conrad, 1837	4(3)	Recent	Pismo Beach, California, U.S.A.
<i>M. (Crenomytilus) grayanus</i> Dunker, 1853	7(6)	Recent	Samani Coast, Samani Town, Hidaka Province, southern Hokkaido, Japan
<i>M. (Tumidimylus) tichanovitchi</i> Makiyama, 1934	8(7)	Takinoue Formation, lower Miocene	Asahi Town, Iwamizawa City, central Hokkaido, Japan
<i>M. (T.) furanuiensis</i> Uozumi and Akamatsu, 1988	6(5)	Furanui Formation, middle Miocene	Hiroto, Monbetsu Town, Hidaka Province, southern Hokkaido, Japan
<i>M. (Plicatomytilus) ksakurai</i> Nomura and Hatai, 1936	22(7)	Isomatsu Formation, lower Miocene	Katsura River, Shiura Village Tsugaru Peninsula, Aomori Pref., northern Honshu, Japan
<i>M. (Plicatomytilus) ksakurai</i> Nomura and Hatai, 1936	32(9)	Furanui Formation, middle Miocene	Kishimatsu-zawa River, Monbetsu Town, Hidaka Province, southern Hokkaido, Japan
<i>Crassostrea gigas</i> (Thunberg, 1793)	1(0)	Recent	Goshiki-hama Coast, Iyo City, Ehime Pref., western Japan









Number of plications	1		2		3	
Ventral view						
Katsura River	3	0	7	5	1	3
Kishimatsu-zawa River	7	4	9	9	0	3

Figure 2. Variation in plication pattern viewed from the ventral side in specimens of *M. ksakurai* from localities in the Katsura and Kishimatsu-zawa Rivers. The number of specimens of each plication type from the two localities is listed in the lower two rows.

detailed characters. 2) is utilized for the base of 3) and 4) to show the position on the commissure.

In this study, aspect b), the whorl expansion rate, is shown as the relationship between the area of the commissure plane (generating curve) and the revolving angle of the commissure plane about the hinge axis (coiling axis). This is not essentially different from the original description of whorl expansion rate in Raup and Michelson (1965). To show this parameter, two variables were measured, 5) revolving angle of the commissure plane about the hinge axis, and 6) area of the commissure plane.

Miocene mytilid species are characterized by their thick shells. Investigation of the change of shell thickness during growth is important to understand the process of their growth. In particular, the change of thickness of the outer part of the fibrous prismatic layer is important, because that is formed following the periostracum and consolidates the shell shape. However, the shell thickness is not useful for precise investigation, because it consists of several internal growth increments that do not all correspond to a single growth stage. Therefore, in this study, parameter c), the index of the secretion rate of the outer part of the fibrous

prismatic layer is introduced. This is defined as the height of a quadrilateral that approximates an internal increment. This index corresponds to the relative secretion rate of an infinitesimal area of the mantle epithelium per one internal growth increment. This is measured as variable 7).

As mentioned above, *M. ksakurai* exhibits wide variation in the number and strength of plications. In this case, it is nonsense to focus only on the number of plications. It is necessary to introduce the index d) degree of plication development. It is natural that when the allometric relationship between the area of the commissure plane and the outline length of the commissure is expressed in a double scatter diagram, the slope of regression abruptly increases after the appearance of plication. The degree of plication development is defined by the angle between two regression lines before and after the plication appears. For this index, 8) outline length of the commissure is measured, and 9) degree of plication development is represented based on variables 6) and 8).

To make a biometric analysis, commarginal growth rings on the shell at different growth stages were marked by attaching narrow adhesive tapes to them. These commar-

Figure 1. Shell morphology of selected Miocene (1–5) and extant (6) mytilids, and *Crassostrea* (7). Lateral (a) and ventral (b) views for 1–6. All at natural size. Arrows point to the allometric critical point for the growth of shell convexity. 1. *Mytilus* (*Tumidimylus*) *tichanovitchi* Makiyama. Lower Miocene Takinoue Formation, Asahi Town, Iwamizawa City, central Hokkaido. UMUT CM 27606a. 2. *Mytilus* (*Tumidimylus*) *furanoiensis* Uozumi and Akamatsu. Middle Miocene Furanui Formation, Hiroto, Monbetsu Town, Hidaka Province, southern Hokkaido. UMUT CM 27607a. 3, 5. *Mytilus* (*Plicatomytilus*) *ksakurai* Nomura and Hatai. Middle Miocene Furanui Formation, Kishimatsu-zawa River, Monbetsu Town, Hidaka Province, southern Hokkaido. UMUT CM 27609a (3) and UMUT CM 27609b (5). 4. *M. ksakurai* Nomura and Hatai. Lower Miocene Isomatsu Formation, Katsura River, Shiura Village, Tsugaru Peninsula, Aomori, North-East Japan. UMUT CM 27608a. 6. *Mytilus* (*Mytilus*) *galloprovincialis* Lamarck. Recent. Nojima Coast, Tokyo Bay, central Japan. UMUT RM 27603a. 7. *Crassostrea gigas* (Thunberg). Lateral view. Recent. Goshiki-hama Coast, Iyo City, Ehime Prefecture, western Japan. UMUT RM 27610.

ginal growth rings are chosen as narrowly as possible. The most distant point from the hinge axis, that is the coiling axis in Raup and Michelson (1965), was marked with a pen for each growth ring. Then, photographs were taken from different directions for each specimen: one from the lateral side, perpendicular to the last-formed commissure plane, one from the ventral margin, parallel to the last-formed commissure plane, and a series of photographs from directions perpendicular to the commissure plane at each growth stage.

Variables 1) to 9) mentioned above were measured. For variables 3) and 4), measurement data are normalized so that the commissure planes of all specimens have the same area as the last-formed commissure plane of the specimen of *M. galloprovincialis* (UMUT RM 27603b).

Detailed methods to obtain the above variables are described below:

1) *Lengths of major and minor axes of the commissure plane approximated to an ellipse.*—These lengths were measured in the specimens of *M. ksakurai* and *M. tichanovitchi*. First, photographs were taken perpendicular to the commissure plane at each growth stage. Images of commissure planes were approximated to an ellipse using the software NIH Image 1.53 (freeware). They were transmitted to a Macintosh computer via an image scanner, and the lengths of major and minor axes were measured using the software NIH Image 1.53 (freeware).

2) *The position of the break point on the commissure.*—The Miocene mytilids examined are generally flat in the juvenile stage, but the curvature of the shell increases abruptly during ontogeny, which causes an inflated shell form in the middle to later growth stages. The commarginal growth line at the stage of the allometric change in shell convexity was photographed for each specimen. On the enlarged photo, the commissure at this stage was divided by a number of chords of equal length (5 mm) using a compass, starting from the beak. The mid-point of each segment of commissure is called the break point (BP, Figure 3A). The

position of the break point on the commissure is defined as the angle β between the hinge axis and the straight-line segment connecting a break point and the mid-point (P) of the hinge line (Figure 3-A). This angle was measured using a protractor. This variable is used as a signpost on the commissure in the graph of variables 3) and 4). The position on the commissure is represented as shown in Figure 3-B.

3) *The distance between the hinge axis and the break point on the commissure.*—This is defined as the perpendicular distance from a break point to the hinge line (d , in Figure 3-A). It is measured (using a slide caliper) from the point at which plications begin to appear, or at the stage of the allometric change in shell convexity.

4) *Curvature of each segment of the commissure.*—Curvature, R is generally defined as:

$$R = d\theta/dl \quad (1)$$

where l is the arc length and θ is the angle between two unit normal vectors. Measurements on actual specimens were made in the following manner (see Figure 3-A).

On the enlarged photo used in the measurement of variable 2), the commissure was divided by a number of chords of equal length (5 mm), using a compass, starting from the beak. When this chord is sufficiently short, it approximates a segment of the commissure. The angle θ_a between each pair of bisectors (a_1 and a_2 , in Figure 3-A) of the angles between neighboring chords (α_1 and α_2 , in Figure 3-A) was measured using a protractor. It is regarded as θ in equation (1). Thus, the curvature (R) of each segment of the commissure (c , in Figure 3-A) was approximated by:

$$R = \theta_a/b$$

where b is the length of a chord.

5) *Revolving angle of the commissure plane about the hinge axis.*—This value at a given growth stage was obtained using the following formula (see Figure 3-C):

$$\varphi_{rot} = \arctan\left(\frac{z}{x}\right)$$

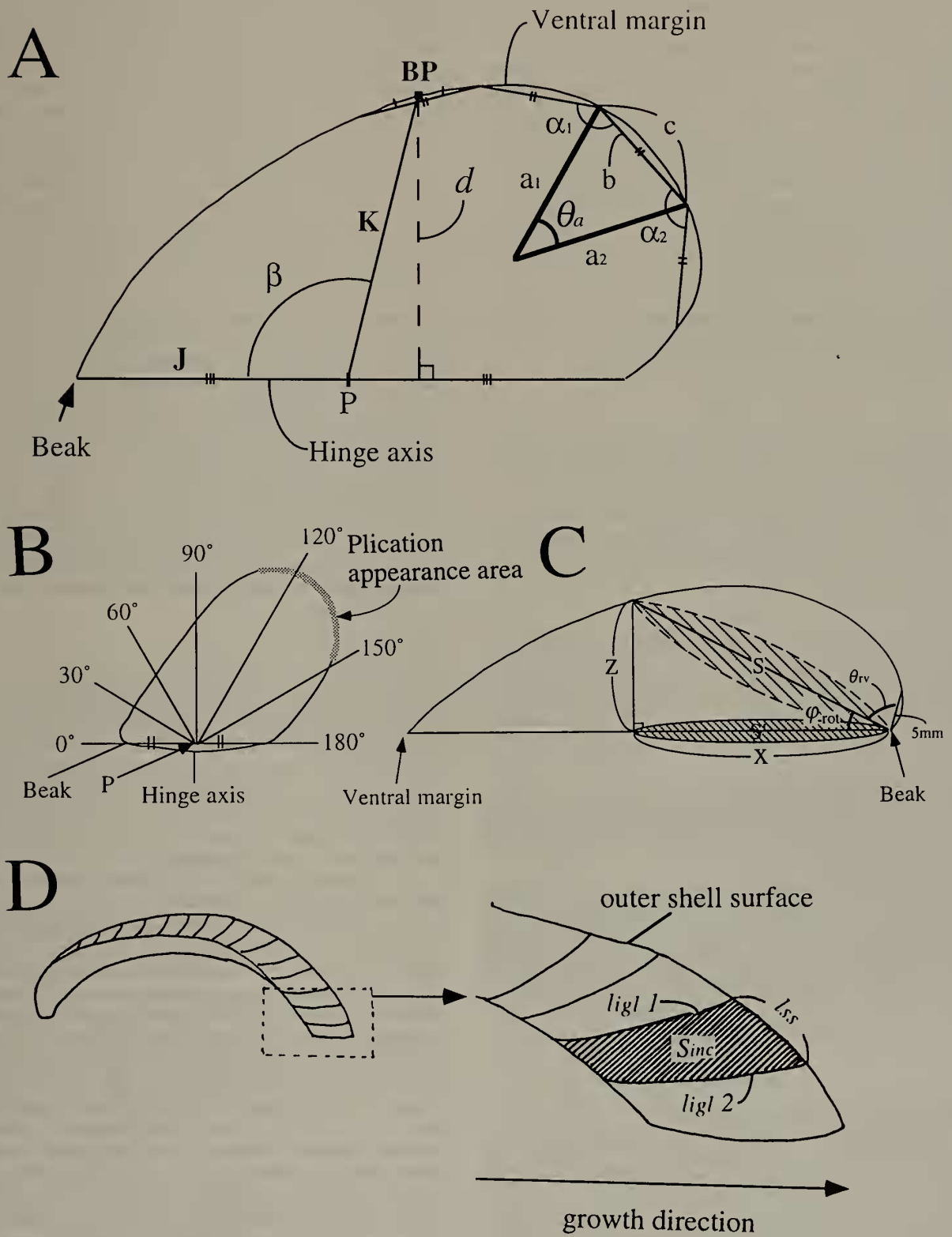
Figure 3. Diagrams showing the methods of measurements.

A: Schematic figure showing the measurements of curvature for each segment of the commissure, the distance from the hinge axis to break point on the commissure, and the position on the commissure. See text for details. This figure shows the shell outline viewed from a lateral direction. b : length of the chord, c : length of the segment of the commissure, BP: break point on the commissure, d : distance from the hinge axis to BP, P: the middle point of the hinge axis, α_1 and α_2 : angles between two neighboring chords, a_1 and a_2 : bisectors of α_1 and α_2 , β : angle representing the position of BP on the commissure, J: segment connecting the beak and P, K: segment connecting P to MP.

B: Schematic diagram showing the position on the commissure. Position on the commissure is represented with the angle as shown in Figure 3-B. Shadowed portion represents the plication appearance area in the shell of *M. ksakurai* at the allometric critical point. P: the mid-point of the hinge axis.

C: Schematic diagram showing the measurement of the revolving angle of the commissure plane and the area of the commissure plane. φ_{rot} : the backward rotation angle from the last-formed commissure plane, z : the perpendicular distance between the last-formed commissure plane and the most distant point (marked point) from the hinge axis in each earlier commissure plane, x : the distance between the projection of that point to the last-formed commissure plane and the hinge axis, θ_{rv} : the revolving angle of the commissure plane, S : the real area of the commissure plane, S' : the projected area of the commissure plane.

D: Schematic figures defining the index of the secretion rate of the outer part of the fibrous prismatic layer. The left figure is a sectioned valve cut along the maximum growth axis. The right figure is a closeup view of the internal growth increments near the ventral margin. I_{igl1} and I_{igl2} : internal growth lines, l_{ss} : the length of the side of the shadowed area along the shell surface, S_{inc} : area of the shadowed area. The index of the secretion rate of the outer part of the fibrous prismatic layer is defined as the height of the quadrilateral approximating the shadowed area.



where φ_{rot} is the backward rotation angle from the last-formed commissure plane, z is the perpendicular distance between the last-formed commissure plane and the most distant point (marked point) from the hinge axis in each earlier commissure plane, and x is the distance between the projection of that point to the plane of the last-formed commissure plane and the hinge axis. The values of z and x were measured on enlarged photographs using a slide caliper and then converted to natural size. The backward rotation angle (φ_{rot}) is finally converted to the revolving angle of the commissure plane (θ_{rv}) measured forward from the earliest shell at a shell length of 5 mm. Conversion from φ_{rot} to θ_{rv} has no biological significance.

6) *Area of the commissure plane.*—Each photographic image of the commissure plane was transmitted to a Macintosh computer using an image scanner, and the projected area of the commissure plane was calculated using the software NIH Image 1.53 (freeware). The projective area was calibrated by the following equation:

$$S = \frac{S'}{\cos \varphi_{rot}}$$

where S is the real area of the commissure plane, S' is the projected area of the commissure plane, and φ_{rot} is the backward rotation angle (Figure 3-C).

7) *Index of secretion rate of the outer part of the fibrous prismatic layer.*—The definition of this parameter has already been mentioned above. This is obtained as:

$$\frac{2S_{inc}}{(l_{igl1} + l_{igl2}) \times l_{ss}}$$

where S_{inc} is the area of the hatched portion in Figure 3-D; l_{igl1} and l_{igl2} are the lengths of two neighboring internal growth lines; and l_{ss} is the increment width on the outer shell surface (see Figure 3-D). S_{inc} was measured using the software NIH Image 1.53 (free ware). l_{igl1} , l_{igl2} , and l_{ss} were measured, using a slide caliper, on the photograph of the sectioned surface of the shell.

8) *Outline length of the commissure.*—The length of an adhesive tape attached to each major growth ring is defined as the outline length of the commissure. It was measured using a slide caliper.

9) *Degree of plication development.*—As already mentioned, this is defined by the angle between two regression lines before and after the plication appearance in the scatter diagram which represents the relationship between the area of the commissure plane and the outline length of the commissure. These two regression lines were calculated with the reduced major axis method.

Results

Morphology of the commissure plane

In *M. tichanovitchi*, *M. furanuiensis*, and *M. californianus*, the outline shape of the commissure plane consists of two straight portions (hinge axis and anterior half of ventral margin) and two sharply curved ones (beak area and rounded ventral end). In these species, the commissure plane approximates an elongated ellipse. The major axis of this

ellipse is nearly parallel to the hinge axis. Therefore, the sharply pointed area with the largest curvature is located near the hinge axis (Figures 1-1a and -2a, and 4-B, C and F). In the later growth stage of *M. furanuiensis*, the ventral margin is curved and the sharply pointed area moves away from the hinge axis as the shell grows (Figure 1-2a). In *M. galloprovincialis* and *M. grayanus*, the sharply pointed area is much closer to the beak and much more distant from the hinge axis than in *M. tichanovitchi*, *M. furanuiensis*, *M. ksakurai* and *M. californianus* (Figures 1-6a, and 4-D, E). However, the curvature of each segment of the commissure of *M. galloprovincialis* and *M. grayanus* is smaller than in *M. tichanovitchi*, *M. furanuiensis*, *M. ksakurai*, and *M. californianus* (Figures 4D and E), indicating that the commissure plane in *M. galloprovincialis* and *M. grayanus* approximates to a short, wide ellipse. The outline shape of the commissure plane in *M. ksakurai* is intermediate between *M. galloprovincialis* and *M. tichanovitchi* (Figures 1-3a and 4-A). The sharply pointed area on the commissure plane in *M. ksakurai* is similar to but slightly closer to the beak than in *M. tichanovitchi* (Figure 4-A and B). The curvature of the sharply pointed area in *M. ksakurai* is slightly smaller than in *M. tichanovitchi*, although the range of this area in *M. ksakurai* is wider than in *M. tichanovitchi* (Figure 4-A and B). Therefore, the ellipse of the commissure plane in *M. ksakurai* is shorter and wider than in *M. tichanovitchi* (Figure 5). The outer shape of the commissure plane in *M. tichanovitchi* tends to be markedly elongated along the maximum growth axis, whereas the degree of shell elongation is weak throughout ontogeny in *M. ksakurai* (Figure 5).

Shell convexity

The Miocene mytilids examined exhibit diphasic shell growth (Figures 1 and 6, Table 2). In the juvenile stage, their shells are thin and weakly convex (having high whorl expansion rate) as in most extant mytilids. Juvenile shells of *M. tichanovitchi* and *M. furanuiensis* are more weakly convex than adult shells of extant mytilids and juvenile shells of *M. ksakurai* (Figure 6, Table 2). The juvenile shell form of *M. ksakurai* is as weakly convex as the adult shell forms of *M. galloprovincialis* and *M. grayanus*.

In the Miocene mytilids examined, shell convexity is low in their juvenile stages but begins to increase markedly in mid-ontogeny (Figures 1 and 6). This allometric change in shell convexity causes an unusually inflated shell form in later stage. This allometric change is very similar to "geniculation" in the Late Cretaceous inoceramid *Cremnoceramus* (Crampton, 1996). This allometric change is especially conspicuous in *M. tichanovitchi* and *M. ksakurai*, but it is only weakly developed and not abrupt in *M. furanuiensis* (Figure 1-2). The shell of *M. furanuiensis* is much less convex than those of *M. tichanovitchi* and *M. ksakurai* (Table 2). The shell convexity of *M. tichanovitchi* is similar to that of *M. ksakurai* (Table 2). However, the ontogenetic change of shell convexity is more conspicuous in the former species than in the latter (Table 2). In both species, conspicuous commarginal ribs resembling steps begin to develop soon after the allometric change in shell convexity (Figure 1-1~5).

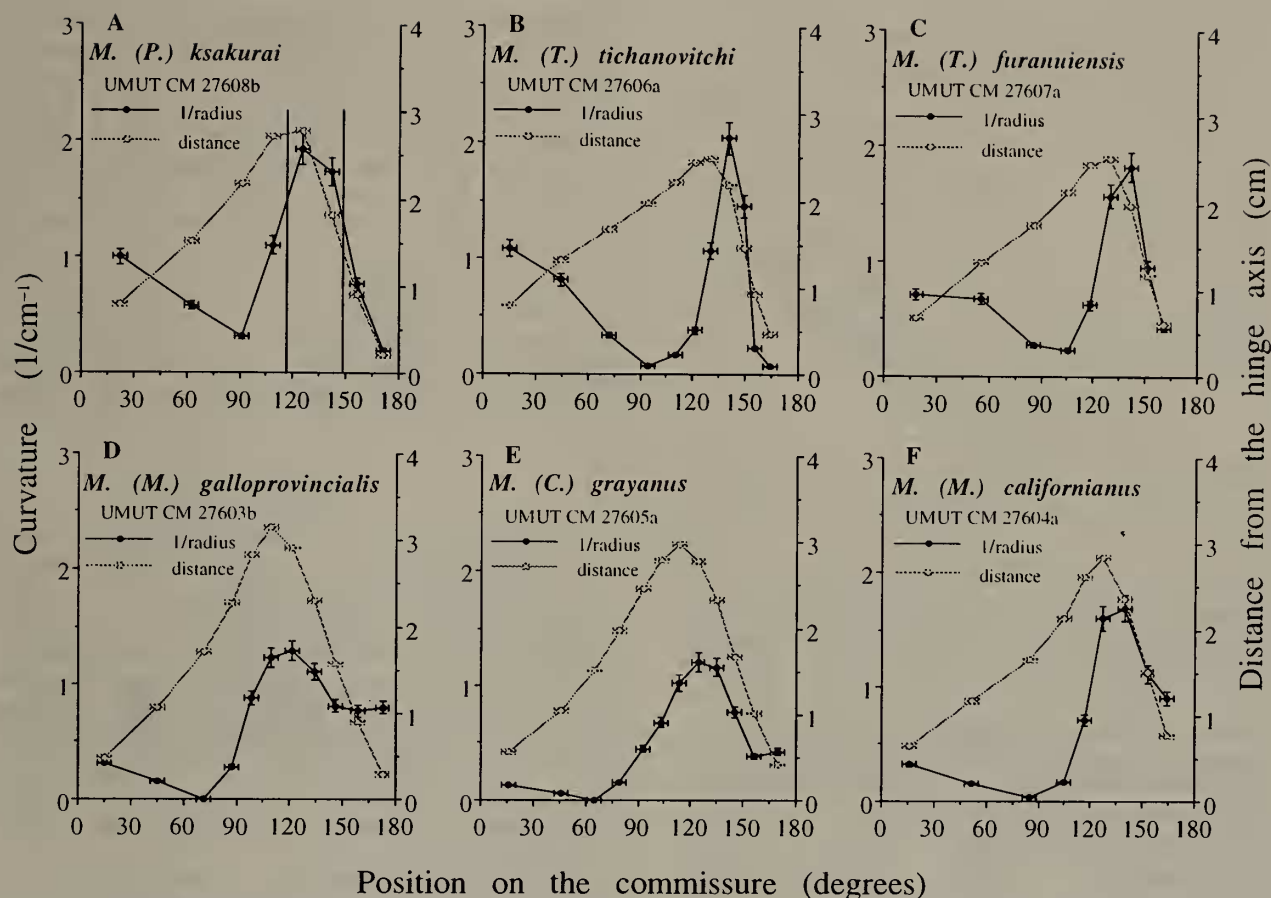


Figure 4. Relationship of the curvature of each segment of the commissure, and of the distance from the hinge axis to the commissure, compared with the position on the commissure in six species of *Mytilus*. The data are based on the measurements of a single specimen for each species. Two vertical lines in the case of *M. ksakurai* (A) represent the area where plications appear (from 117° to 148°).

Mode of shell secretion and expansion

In order to understand the relationship between increasing shell convexity and shell thickness, polished sections of selected specimens were observed under a microscope. In specimens of *M. grayanus* and *M. ksakurai*, each internal growth increment in the outer part of the fibrous prismatic layer is widest on the outer shell surface and narrowest just above the boundary with the inner part of the fibrous prismatic layer (Figure 7). *M. grayanus* does not exhibit any remarkable ontogenetic change in the growth pattern of internal growth increments (Figure 7-A). This is true also for *M. galloprovincialis* and *M. californianus*. In contrast, internal growth lines in *M. tichanovitchi*, *M. furanuiensis*, and *M. ksakurai* all bend toward the inside of the shell as if the pallial line were a fulcrum at the stage of the allometric change in shell convexity (Figure 7-B).

In *M. ksakurai*, the secretion rate of the outer part of the fibrous prismatic layer in the stage before the allometric change in shell convexity is low (index of shell secretion rate about 0.2, Figure 8-B). In this stage, the shell expands ventrally, maintaining low convexity (Figure 6-C). The index increases to 0.35 near the stage of allometric change in shell

convexity and attains a maximum (0.55) at the stage of the allometric change (Figure 8-B). After the abrupt change in shell convexity, this index fluctuates between about 0.2 and 0.7 (Figure 8-A). This causes the development of steplike growth rings on the shell of *M. ksakurai* and in all the other Miocene mytilids examined here (Figure 1-1-5). In general, the index of the secretion rate is small in the juvenile stage but increases abruptly soon after the stage of the allometric change in shell convexity (Figure 8). The whorl expansion rate after the stage of the allometric change in shell convexity is much lower than before this allometric change (Figure 6, Table 2). This produces a thick, highly convex shell. In both *M. tichanovitchi* and *M. ksakurai*, the conspicuous ontogenetic change in inclination of microincrements corresponds to the stage of the allometric change in shell convexity. In contrast, in *M. furanuiensis*, the conspicuous change of inclination of microincrements occurs in later growth stage after the allometric change in shell convexity, following the initiation of the step-like commarginal ribs in cross section. Therefore, in this species, the allometric change in shell convexity is not so conspicuous and the shell form becomes markedly elongated and weakly inflated later in ontogeny.

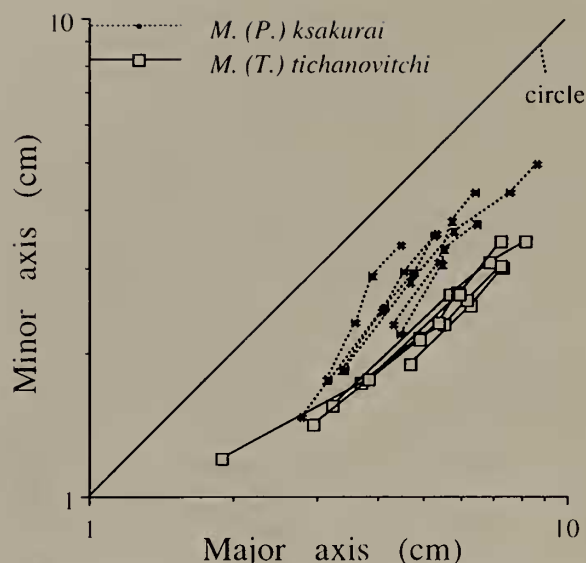


Figure 5. Ontogenetic allometric relationship between major and minor axes of the generating curve for selected specimens of *M. ksakurai* and *M. tichanovitchi*.

Table 2. Average of the slope of the regression line in double scatter diagram of the allometric relationship between the square root of the area of the commissure plane and the total revolving angle of the commissure plane.

species	stage	av	N	SD
<i>M. (T.) tichanovitchi</i>	juvenile	24.120	7	7.337
	adult	155.532	7	23.133
<i>M. (T.) furanuiensis</i>	juvenile	18.341	1	
	adult	101.838	4	42.570
<i>M. (P.) ksakurai</i> (Katsura River)	juvenile	56.437	7	18.154
	adult	114.987	7	35.927
<i>M. (P.) ksakurai</i> (Kishimatsu-River)	juvenile	38.480	7	18.480
	adult	157.530	9	49.623
<i>M. (C.) grayanus</i>		49.525	6	13.223
<i>M. (M.) galloprovincialis</i>		45.285	6	3.526
<i>M. (M.) californianus</i>		72.501	3	17.803

av: average of slope, N: number of specimens,
SD: standard deviation

(Figure 1-2).

Plication morphology

In *M. ksakurai*, the stage of the allometric change in shell convexity corresponds with the abrupt appearance of plications (Figure 1-3, -4, and -5). Large samples from localities in the Katsura and Kishimatsu-zawa Rivers show remarkable individual variation in the number of plications, and the pattern of undulations in the commissure is not uniform among specimens with the same number of plications (Figure 2). In general, the variation in the number of plications is regarded as a discrete distribution, because the number of plications is not a decimal but an integer. However, in view of the degree of plication development, plications show continuous variation (Figure 9). Therefore, continuous variation in excessive expansion of the mantle edge appears as

discrete variation in the number and pattern of plications. In spite of the wide variation in their number, pattern, and degree of development, plications in *M. ksakurai* begin to appear in a restricted area on the commissure at the stage just before the allometric change in shell convexity (between 110° and 150° in the angle measured from the standardized point P in Figure 3-B; see Figure 1-3a, -4a, and -5a). The index of shell secretion rate at a given shell size is measured in the portion of ridge and sulcus. In both portions, this index fluctuates between about 0.2 and 0.7 (Figure 8-A). The range of the fluctuation of this index in the portion of the ridge does not differ clearly from that in the portion of the sulcus. Therefore, it can be said that the index of shell secretion rate at a given shell size does not differ between ridge and sulcus (Figure 8-A).

Discussion

Several explanations have been proposed for the formation of patterns of radial and spiral sculpture in molluscs. Cox *et al.* (1969) and Hayami (1974) speculated that radial costae and striae in bivalves result from the enhanced secretion of calcium carbonate by groups of cells perpendicular to the mantle margin. According to their hypothesis, the shell sculpture would consist of thick ridges and relatively thin furrows. However, in the examined specimens of *M. ksakurai*, no significant difference in the index of the shell secretion rate occurs between ridge and sulcus (Figure 8A). This suggests the absence of perpendicular cells along the mantle margin.

Seilacher (1985) suggested that the divergent plications of ostreids, malleids, and anomiids are produced by excessive tangential growth of the mantle edge. The existence of divergent plications on the shell implies an excess of mantle in relation to shell edge. However, the plication of *M. ksakurai* is distinguished from that of ostreids and malleids by its association with allometric changes in shell convexity and a subsequent abrupt shell thickening (Figures 1-3, -4, and -5, and 7-B). In *M. ksakurai*, the development of plication is restricted to part of the shell margin (between 110° and 150° in the angle measured from the standardized point P in Figure 3-A, Figure 1-3a, -4a, and -5a), whereas in ostreids, malleids, and anomiids, plications are developed over the whole shell surface (Figure 1-7). Moreover, in extant Bivalvia, a relative increase of shell convexity is, in most cases, caused by a reduction in the mantle proliferation rate (Seed, 1968; 1980; Vermeij, 1990). Therefore, the mantle proliferation rate of *M. ksakurai* presumably decreased after the allometric change in shell convexity. In this species, excessive tangential growth of the mantle edge might not have occurred when plications appeared.

To generate the excess of mantle margin relative to the shell edge without acceleration of mantle proliferation, the space in which the mantle can be accommodated must be reduced. Internal growth lines conspicuously turn inward after the allometric change in shell convexity. This suggests a bending of the distal part of the mantle (Figure 7-B). If a curved surface or a plane with a curved perimeter is bent inward along its edge, the distal part of that plane surface

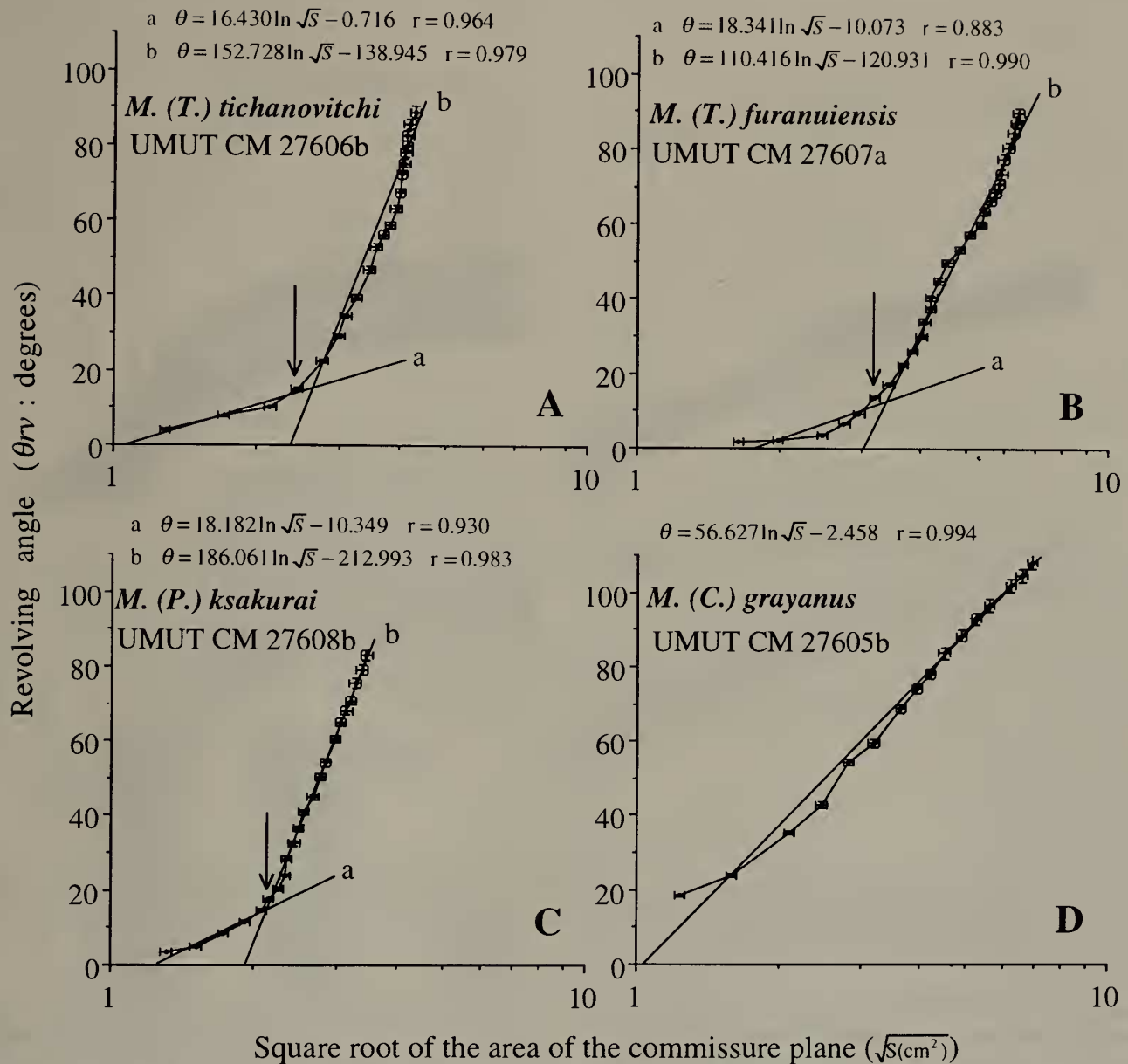


Figure 6. Ontogenetic allometric relationship between the area of the commissure plane and the revolving angle of the commissure plane in three Miocene mytilids (A–C) and one extant one (D). Each graph is based on a single specimen. Arrows in A–C point to the stage of the allometric change in shell convexity. Regression lines a and b were calculated by the least squares method.

must be deformed and wrinkled, because this portion, including the edge, is compressed into a narrower space. This leads to the prediction that the mantle edge will be deformed and wrinkled when the distal part of the mantle is bent. This type of plication is analogous to the wrinkles of the skirt of a tablecloth (Figure 10), so this model is called here “the tablecloth wrinkle model”. This explanation has already been applied to plate tectonics under the name spherical shell tectonics (Bayly, 1982; Yamaoka, 1984, 1988). In the case of tablecloth wrinkles, the bending force is gravity. In the case of the mantle of *M. ksakurai*, it is inferred to be the

adhesive force of the mantle to the inner shell surface. The changed direction of this force would result from abrupt shell thickening, due to a rapid increase in the rate of shell precipitation relative to the whorl expansion rate (Figures 7–B and 8–B).

In the case of a bivalve mantle, space reduction derived from mantle bending is greatest when 1) the mantle bending angle is large, or 2) the curvature of the margin of the commissure is large, or 3) the distance of the area of bending from the mantle edge (the distance from the mantle edge to the pallial line) is large (Yoshida, 1996). The mantle

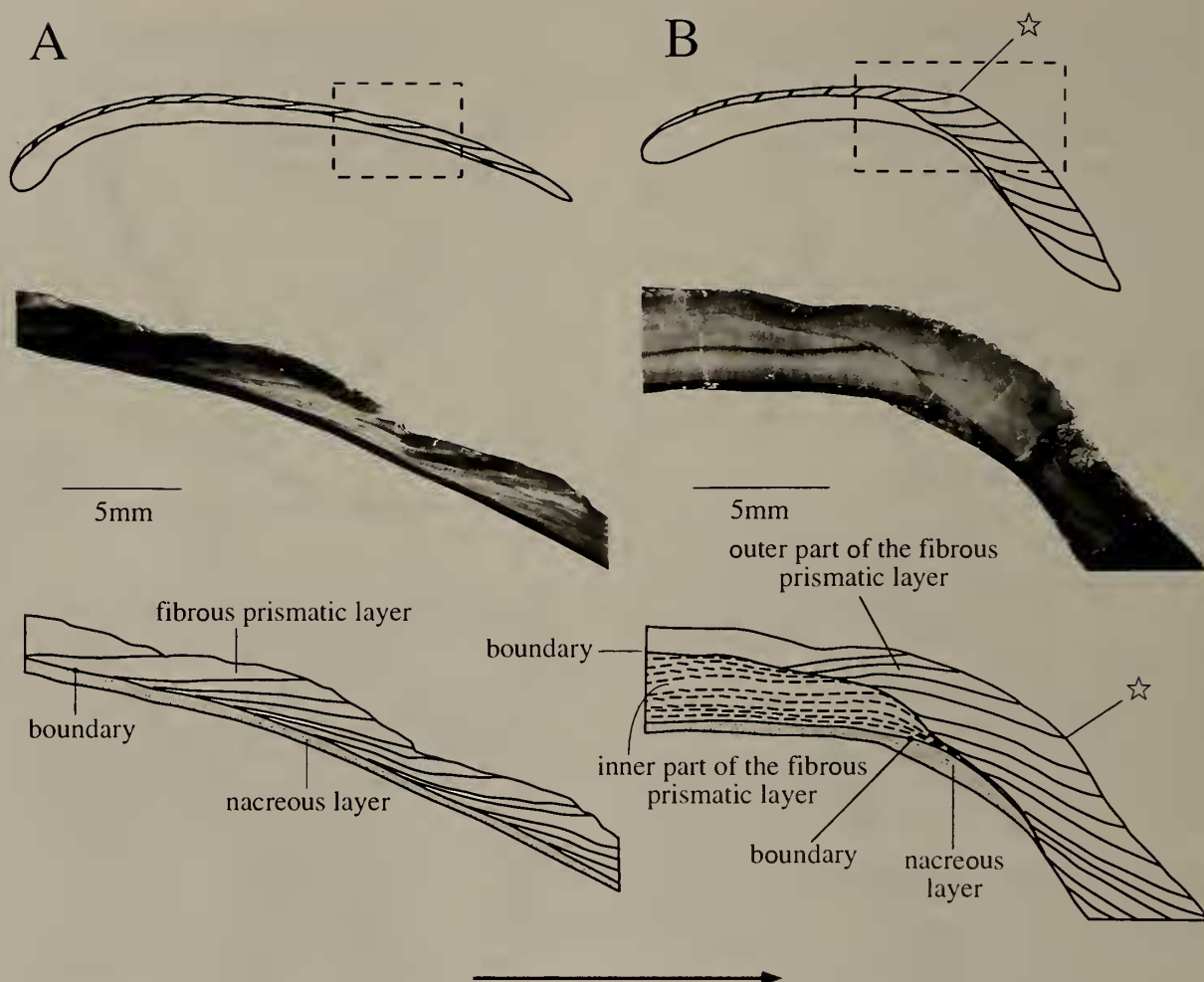


Figure 7. Photomicrographs and sketches of the middle shell portion cut along the maximum growth axis of *M. grayanus* (A : UMUT RM 27605c) and *M. ksakurai* (B) UMUT CM 27608c). The stars in B indicate the stage of the allometric change in shell convexity.

bending angle is large where there is a high shell secretion rate, because here shell thickness is large, and the mantle has to be bent inward at a large angle to adhere to the inner shell surface. In most bivalves, the shell secretion rate has to be in proportion to the distance from the hinge axis, because they could not otherwise close their shell completely. Therefore, the mantle bending angle is in proportion to the distance from the hinge axis. The condition 1) can also be expressed in the words, "when the distance from the hinge axis is large".

As already noted, plications do not appear in *M. furanuiensis* and the three extant mytilids examined. In these species, mantle bending may not occur because of the absence of a conspicuous allometric change in shell convexity. In *M. ksakurai*, plications appear in the area between the point most distant from the hinge axis and the point having the largest curvature (between 110° and 150° in rotation angle measured from the standardized point P) (see Figures 3-A and 4-A). Following the tablecloth wrinkle

model, the mantle is pushed into a narrower space here than elsewhere. This model may explain the remarkable variation in the degree of plication in *M. ksakurai* (Figure 9), since it is determined mainly by the shape of the commissure plane and the degree of mantle bending, which may vary independently of one another. This model may also be applied to the nature of the variation of plication in *M. ksakurai*. Following this model, the pattern of plication is determined by the excess of mantle via the nonlinear process of buckling of the mantle. The excess of mantle derived from mantle bending may have a continuous variation. Therefore, in *M. ksakurai*, the degree of plication exhibits a continuous variation, although the pattern of plication has a discrete variation.

Under this model, growth of *M. tichanovitchi* should have involved a higher degree of space reduction than in *M. ksakurai*, in view of its more conspicuous allometric change in shell convexity (Figures 1 and 6, Table 2) and larger curvature of the ventral margin of the commissure (Figure 4).

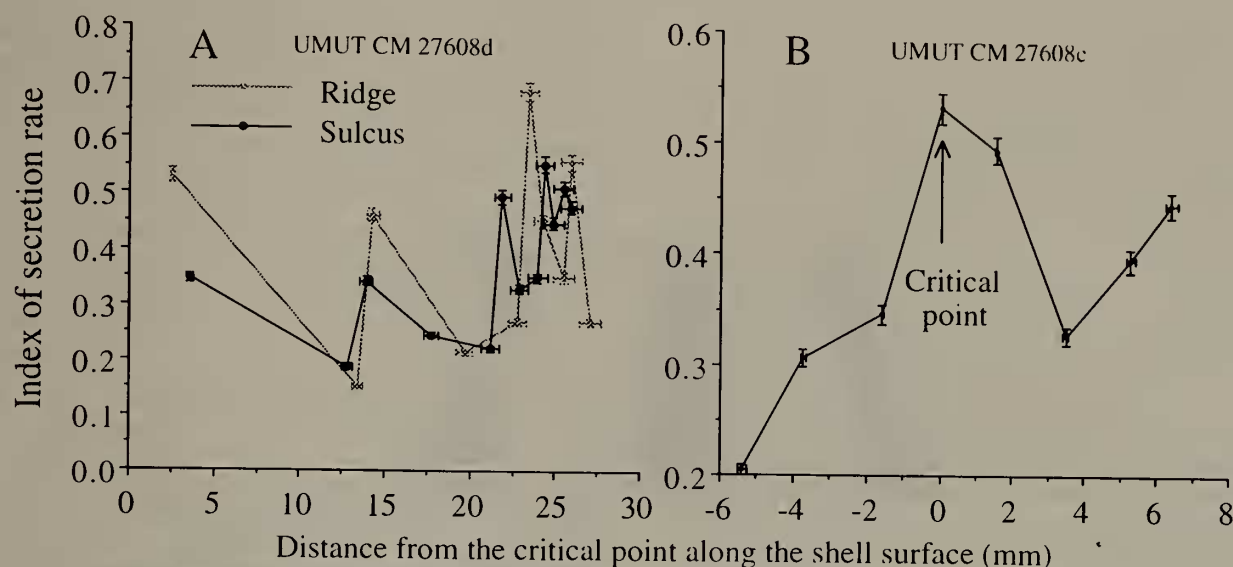


Figure 8. Index of shell secretion rate of the outer part of the fibrous prismatic layer in two specimens of *M. ksakurai*. **A:** Comparison between ridge and sulcus. UMUT CM 20608d from the lower Miocene in the Katsura River. **B:** Change of the index of secretion rate around the allometric critical point. UMUT CM 20608c (same specimen as shown in Figure 7B).

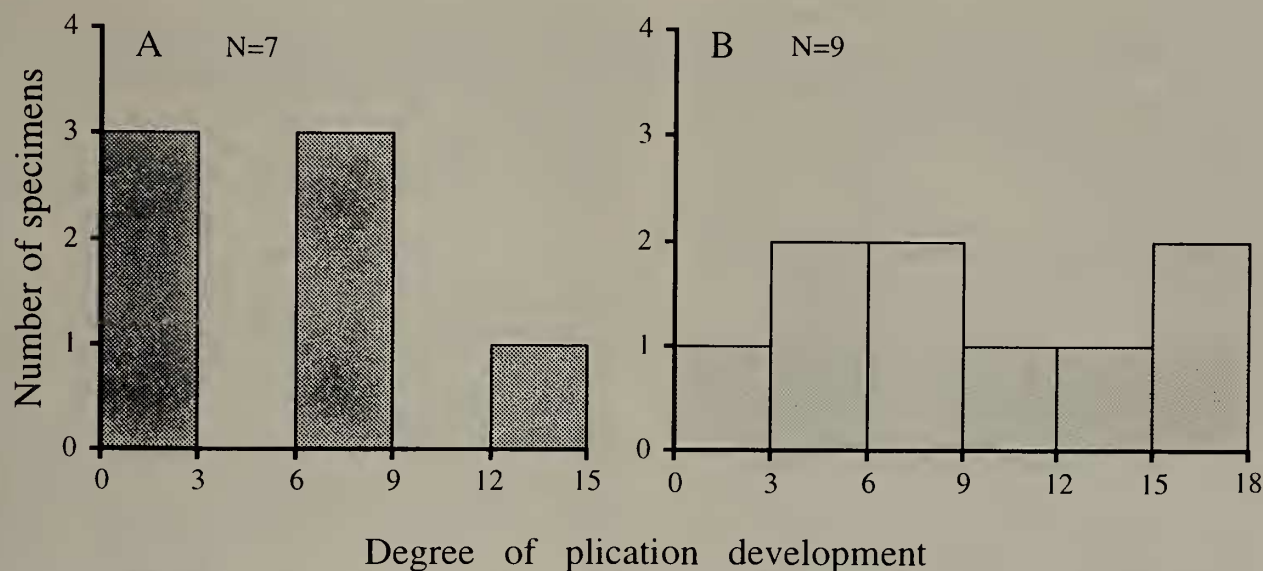


Figure 9. Variation of the degree of plication development in the samples of *M. ksakurai* from the localities in the Katsura (A) and Kishimatsu-zawa (B) Rivers. The variations of the two samples overlap each other.

In Yamaoka's (1984) experiments on transformation of a cylindrical elastic body, wrinkles with a large wave length are stable under a high degree of space reduction. A similar phenomenon appears to occur in the bending of the elastic bivalve mantle. In *M. tichanovitchi*, with a high degree of space reduction, a single large wrinkle (indicated by the bold line in Figure 11-A) is more stable than several small wrinkles (indicated by the dotted line in Figure 11-A). This produces a new force indicated by the arrow in Figure 11. The vector of this force is oriented obliquely to the commissure plane and roughly parallel to the hinge axis (see Figure 11B). The

vector has components parallel to and perpendicular to the commissure plane. The perpendicular component of this vector makes the shell shape of *M. tichanovitchi* highly convex (Figure 1-1b, Figure 6, Table 2), whereas the parallel one makes it elongated and straight (Figures 1-1a, and 4, and 5). Therefore, the narrowly rounded posteroventral margin of *M. tichanovitchi* itself may represent a single large plication under the condition of a very high degree of space reduction.

The subgenus *M. (Plicatomytilus)* has been distinguished from other mytilid subgenera by differences in the patterns of retractor muscle scars (Allison and Addicott, 1976). How-

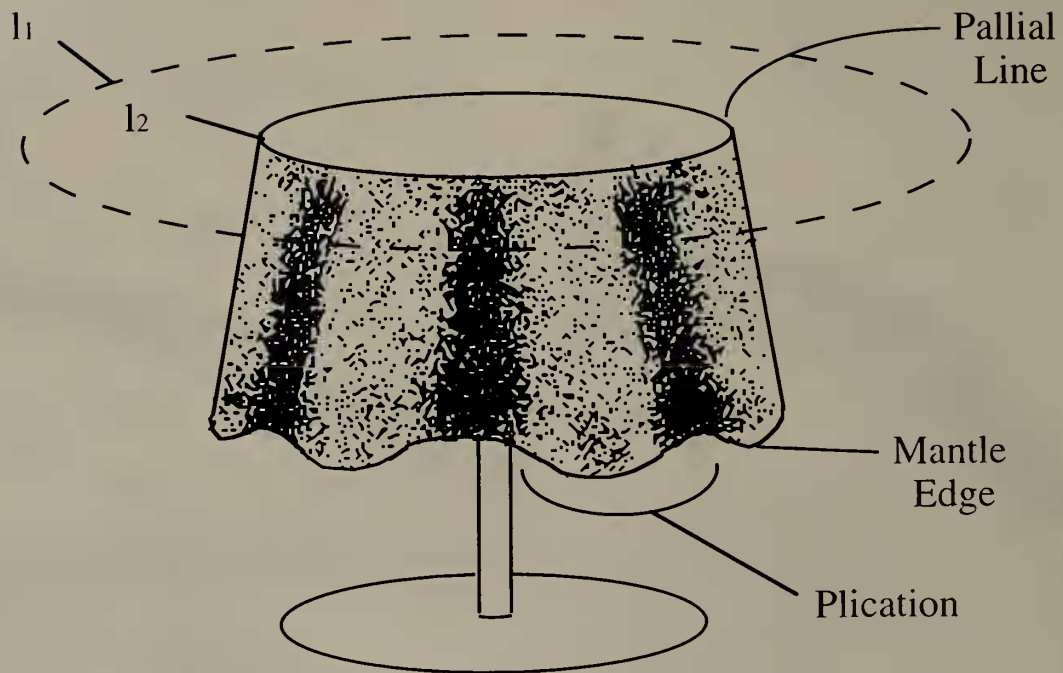


Figure 10. Schematic figure showing tablecloth bending. The tablecloth is bent by gravity along the table-edge. The larger circumference l_1 is pushed into the smaller circumference l_2 , and as a result, the table cloth edge is transformed to a wrinkled state.

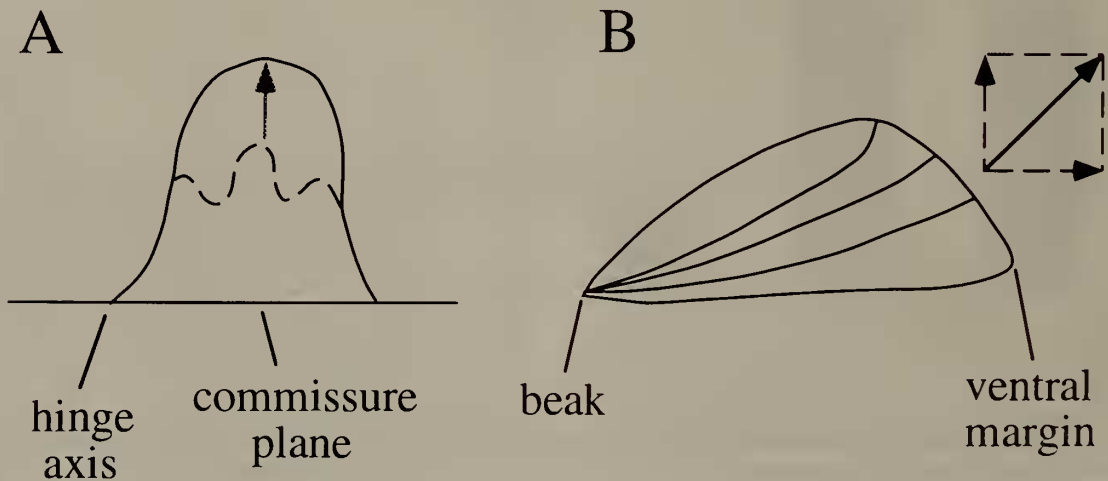


Figure 11. Schematic diagrams showing the effect of mantle bending in *M. tichanovitchi*. The solid arrows represent directions of force under the condition that a large single wrinkle is stable. The diagram A shows a posterior view of the valve. The vector represents the new force that occurs when the mantle shape undergoes a transition from the unstable several wrinkle state to the more stable single wrinkle state via the buckling process. As shown in B, this vector is divided into two directions that are parallel and perpendicular to the commissure plane (B).

ever, Noda and Hoyanagi (1993) suggested that *M. (Plicatomytilus)* is closely related to *M. (Tumidimylus)* in the shape of its anterior byssal retractor muscle scars. If this is correct, the marked morphological discontinuity between the

plicated form (*M. (Plicatomytilus)*) and nonplated form (*M. (Tumidimylus)*) appears to have originated from a slight change of geometric parameters during ontogeny.

As already mentioned, Seilacher (1985) pointed out that

divergent plication in bivalves can be achieved by excessive tangential growth of the mantle margin. However, the tablecloth wrinkle model suggests that in *M. ksakurai*, the excess mantle margin arose from a reduction in space resulting from mantle bending. McGhee (1978) investigated a hypothetical shell growth model and said that changes in whorl expansion rate and increment magnitude along the shell margin should produce irregularity along the commissure margin. In the case of *M. ksakurai*, the irregularity along the commissure margin was produced as a result of the collapse of the equilibrium between the whorl expansion rate and the shell secretion rate.

This study shows that the development and wide variation of plication in the shell of *M. ksakurai* are constrained mainly by an architectural factor (Bautechnischer Aspekt: Seilacher 1970; structural factor: Raup, 1972; "Can the machine be built?": Thomas, 1979; fabrication factor: Seilacher, 1991) derived from mantle bending. The bivalve shell is built as if by stacking of layers in the revolving commissure plane (Lison 1949; Raup and Michelson, 1965; Bayer 1978). Likewise, plication in *M. ksakurai* is created by stacking of layers in a distorted commissure plane.

It is important in constructing theoretical models of morphology to conceive of hard tissue construction in relation to mantle behavior (Savazzi, 1995). This paper proposes a plausible geometric model for plication formation in *Mytilus* (*Plicatomytilus*), without discussing physical properties of the mantle such as elasticity or viscosity. Study of these properties of the mantle during the growth of living bivalves will provide a reliable biophysical basis on which to consider the morphogenesis of molluscan hard tissues.

Acknowledgments

I thank Kazushige Tanabe, Takashi Okamoto, Takao Ubukata, and Roger D.K. Thomas for their enthusiastic guidance and critical reading of the first draft, Itaru Hayami, Tatsuo Oji, Kazuyoshi Endo, Akira Tsukagoshi, Shin'ichi Sato, Taro M. Kiso, Rihito Morita, Sinji Isaji and anonymous reviewers for useful discussion and comments, Yoshikazu Noda for kind advice about taxonomy and help in the field, and Yoshiyuki Fukuzawa for giving me an opportunity to observe type collections housed in Hokkaido University in his care.

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